

BEHAVIORAL STEREOTYPY IN BIRDS

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It has previously been argued that the climatic stability provided by the tropics allows animals to specialize to an extent not possible where climatic conditions and the sources of food and other necessities change seasonally, if not daily (see Klopfer, 1962 for bibliography). This permits the coexistence of more species than would be true in a population of "jacks-of-all-trades," and partially explains the greater faunal diversity of the tropics as compared with temperate zones.

I have sought to put this notion to an experimental test by comparing the degree of behavioral stereotypy (which is, in effect, a measure of niche size: the larger the niche the less stereotyped the animal) in selected representatives from the temperate and tropical avifaunas. The demonstration of stereotypy, of course, does not necessarily prove that constancy of available sources of energy explains species diversity. Greater stereotypy in tropical forms would provide collateral evidence for the constancy-diversity relationship, however.

Specifically, I have sought to measure degrees of stereotypy in foliage preference and motor pattern of individuals of several species of birds. (The ultimate aim, it should be added, is to include several dozen species, representing many families, in this survey, and to include measures other than foliage preferences and movement patterns.)

Regarding the relevance of measures of foliage preference, consider the work of MacArthur, MacArthur, and Preer (1963) who studied early seral stages in North America. They predicted the bird species diversity as well as the actual species which would be present in a given area from measurements of diversity in foliage height density. They showed that each bird species occurred in habitats with a characteristic proportion of foliage in each of three arbitrarily designated layers. These preferences can reasonably be assumed to be based upon either leaf number, leaf size, or leaf shape, or some correlate of these variables, since they alone determine foliage density. Thus, the work of MacArthur, et al. justifies the use of leaf shape and size as the principal discriminanda in studying perceptual preferences. Of course, there are bird species for whom some other and very particular element of the environment such as an unique nest site or particular food will be more important than the characteristics of the foliage density. In most instances these exceptions can be noted. Nor does the importance of foliage characteristics mean that other components of the environment are irrelevant. However, we can at least assert that foliage characters are an important factor in habitat selection.

Other factors than constancy of energy source may influence the degree of stereotypy. Most conspicuous among these is the role of competition, e.g., the number of potentially competing species. On islands or other geographically or topographically isolated areas the species diversity may be well below that of comparable areas of large continental land-masses (see MacArthur, 1965). In the absence of competitors, the ecology of many species is known to change (Crowell, in press, and see van Valen, 1965) generally in the direction of increased plasticity (van Valen, 1965). This increased plasticity may have two different manifestations: each individual of the species concerned may become more plastic, i.e., do more different things, or, the individuals may remain as stereotyped as ever, but with different individuals specializing for different ways of life, or a combination. This would represent decreased specific (as opposed to individual) stereotypy, and might well be regarded as a first stage in the formation of subspecies.

It is as interesting to assess the interaction between degree of isolation (or competition) and climatic stability as to study the latter alone. Thus, our design calls for comparisons between insular and continental birds of the tropics and temperate regions, as diagrammed below:

	Islands	vs	Continents
temperate	Bermuda		Eastern U.S.
vs			
tropical	West Indies		Panama

DEFINITIONS AND METHODS

“Behavioral stereotypy” refers both to perceptual and motor stereotypy. On the perceptual side, the stereotypy involves a sensitivity to, or an awareness of, or preference for, a limited range of a larger complex of stimuli. An animal that responds only to a narrow band of wavelengths, for instance, would be considered perceptually more stereotyped than one responding to a wider band. On the motor side, stereotypy refers to the availability of only a small variety of movements by means of which an animal can accomplish a given act. It reflects an inability to adjust movements in accordance with changes in the form of the substrate. In either instance, the constraints may be peripheral (in terms of muscle attachments or shapes, or sensory filters), or due to central nervous mechanisms. While it is of interest to study the nature of the constraints and to determine whether they differ systematically, this is not considered here.

To measure stereotypy in preferences for particular types of foliage the birds were tested in rooms divided by netting into two chambers, alike except for the foliage with which they were decorated. This foliage was made of a green plastic and consisted of one of 4 kinds of “leaves” that differed

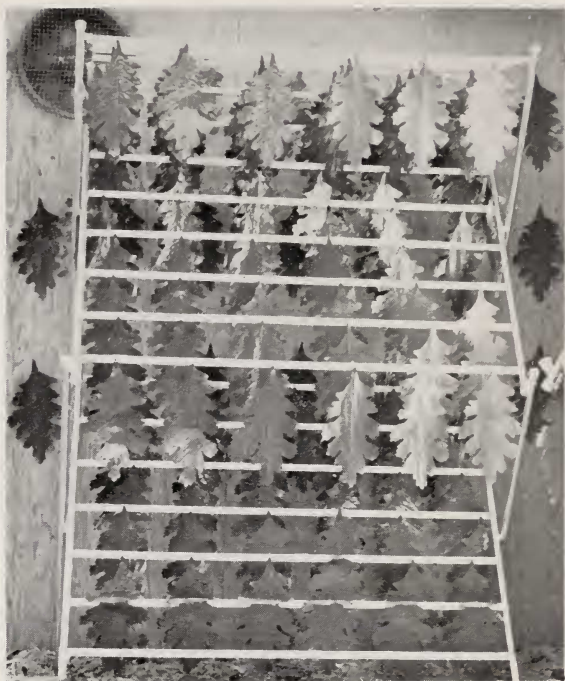


FIG. 1. Photograph of artificial leaves.

in size or shape or density (a large and small "Oak" and "Elm" type) (Fig. 1). Movement of the bird from one chamber to the other, and thus the time spent in each chamber, was monitored by a series of photo-cells in the sole connecting passage between the two chambers, which also served as a feeding place. The three test rooms averaged 3 by 3 by 4 meters. Details of the procedure and controls for position preferences have previously been published (Klopfer, 1965).

The four foliage types employed were offered in all possible pairs, though because of escapes or mortality, every bird was not tested with every pair. For each pair of foliage types, the portion of time spent amidst one or the other was calculated and converted to a discrimination index, \bar{H} . The rationale for the use of the index has been summarized as follows (Klopfer, 1965): the more stereotyped the preferences of an organism, the more marked will be its preferences among an array of discriminanda. If the discriminanda are paired, a non-stereotyped or plastic individual should select each member of each pair, 50 per cent of that time. A highly stereotyped individual will tend to select one member of many pairs to the exclusion of the other. The greater the stereotypy the higher the proportion of pairs

TABLE 1

Species	Rearing conditions	<i>H</i> of individual birds (<i>H</i> values are means for tests with 4 pairs of foliage; \bar{H} are the means of the individual <i>H</i> values)	
Panamanian tanagers (<i>Thraupis cana</i> , and <i>Ramphocelus</i> <i>dimidiatus</i>)	Hand-reared: without sight of foliage	0.06, 0.08, 0.09, 0.14, 0.28	($\bar{H} = 0.13$)
	Hand-reared: with pine needles	0.08, 0.12, 0.28, 0.31	($\bar{H} = 0.20$)
	Wild-trapped:	0.16, 0.17, 0.19, 0.19, 0.20	
		0.20, 0.21, 0.25, 0.25, 0.28 0.30, 0.32, 0.36	($\bar{H} = 0.24$)
Dominican Bananaquits (<i>Coereba flaveola</i>)	Wild-trapped:	0.12, 0.12, 0.18, 0.21, 0.27, 0.31	($\bar{H} = 0.20$)

for which the choice should deviate from 50 per cent. The stereotypy index, *H*, represents the proportion of choices that deviates from 50 per cent. Of course, if a bird selects its habitat using one clue only, for instance light intensity, it would in fact be stereotyped but not so labelled on the basis of tests with irrelevant discriminanda. Thus far, the extremes of \bar{H} values recorded have been 0 and 0.8 (see below).

Motor stereotypy was assessed in two different ways. First, by slow motion analysis of movie film of foraging movements of birds in their natural habitat, taken at varying times throughout the day. Secondly, by observation of the movements of captive birds on artificial "trees." These "trees," ca. 2 m high and varying from ca. $\frac{2}{3}$ m to 2 m in diameter from top to bottom, were constructed of 0.5 cm steel reinforcement rods so as to allow the bird to fly in either a radial, vertical, or horizontal direction without hindrance. (By radial flight is meant flight along a branch, by vertical movement, across branches and in the vertical plane, and similarly, across the horizontal plane for horizontal or oblique flight.) Thus, the environmental constraints upon certain kinds of flight that are posed, for instance, by the thick horizontal strata of foliage or an absence of horizontal branches on some large cacti, were eliminated. The degree of motor plasticity of the subjects could be assessed (even though arbitrarily) under conditions where all three components of the normal flight directions of birds were equally possible. A stereotyped individual, then, would be one which failed to adapt its pattern of flight to this relative absence of physical constraints. Scoring was achieved by simply calculating the proportion of time spent flying in one or other of these planes.

The laboratory and some of the field data were obtained from three tropical species. Blue and Crimson-backed tanagers (*Thraupis cana* and *Rampho-*

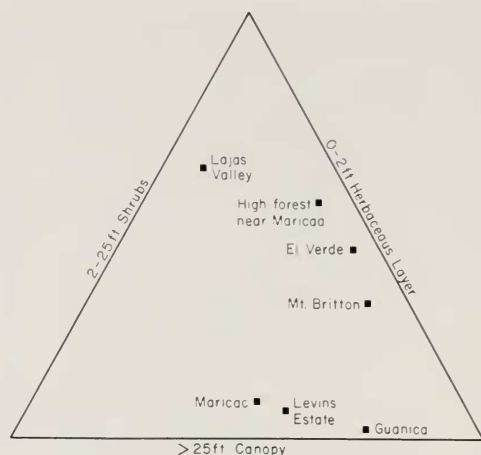


FIG. 2. Habitats in Puerto Rico in which Bananaquits are among the three most common species (after MacArthur).

celus dimidiatus), and the Bananaquit (*Coereba flaveola*). Some of these birds were wild-trapped as adults, others were hand-reared, either without sight of foliage or with a particular kind of foliage. (Comparable data have been previously published for groups of hand-reared and wild-trapped Chipping Sparrows (*Spizella passerina*) and others, Klopfer, 1962, 1965.) The Bermuda field data are taken from the work of Crowell (1962) on the feeding and behavior of Cardinals (*Richmondia cardinalis*) and Catbirds (*Dumetella carolinensis*) and vireos (*Vireo griseus*).

The inadequacy of the sampling and our frequent inability to apply statistical measures of significance, will be apparent. It is the result of the excessive amount of time required for hand-rearing birds from an early age to maturity. The justification for presenting such incomplete data lies (1) in the importance of the general problem and (2) in the desire that this approach may become known to and explored by others.

DATA AND CONCLUSIONS

Perceptual preferences of tropical mainland (Panama) species.—The data of Table 1 suggest that these tropical birds are not innately stereotyped. If reared for the first 8 weeks of life in a particular type of foliage they become more stereotyped. Wild-trapped adults are yet more stereotyped. Of the hand-reared birds, only three out of nine of the tanagers showed scores overlapping with those of any of the 13 wild-trapped tanagers. Most of the hand-reared birds had scores very much below those of the wild birds (i.e., they were less discriminating in their foliage choices).

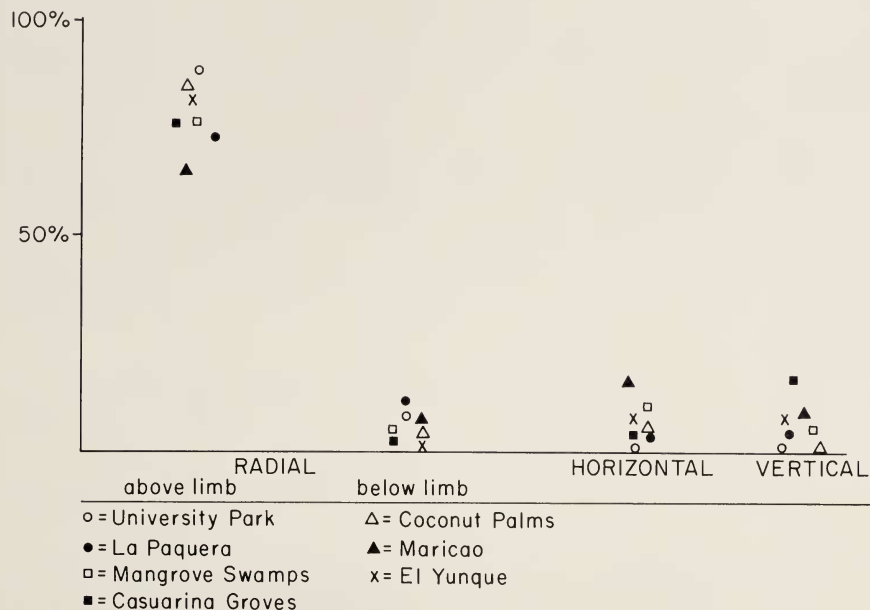


FIG. 3. Movement stereotypy of Puerto Rican Bananaquits.

Perceptual preferences of tropical island (West Indies) species.—Figure 2 indicates the character of the habitats of Puerto Rico in which Bananaquits are among the three commonest birds (the data for this figure were generously provided by R. H. MacArthur). From the variety of habitats in which they occur, it will be apparent that, if Bananaquits can in any way be considered “stereotyped,” this is not manifested by their restricting themselves to any particular plant formation. Is it possible that they are responding to some feature common to all of the habitats in which they are found, and lacking in those habitats where Bananaquits do not occur? Table 1, which provides the data from foliage preference experiments with Dominican, wild-trapped Bananaquits (on Dominica, Bananaquits are also found at all altitudes and in most habitats, as on Puerto Rico) shows a rather low discrimination index (ranging from 0.12 to 0.31). Particular leaf shapes or sizes are apparently no more rigidly preferred than is the case with the relatively “plastic” hand-reared isolates of the other species tested, whether from tropical or temperate zones. In an experiment where the choice was between two different *densities* of the same foliage (artificial bamboo), a similarly low index obtained (0, 0.03, 0.14, 0.30, and 0.33), indicating that leaf density, per se, was not by itself important for three out of the five birds. Another experiment in which the Bananaquits could choose

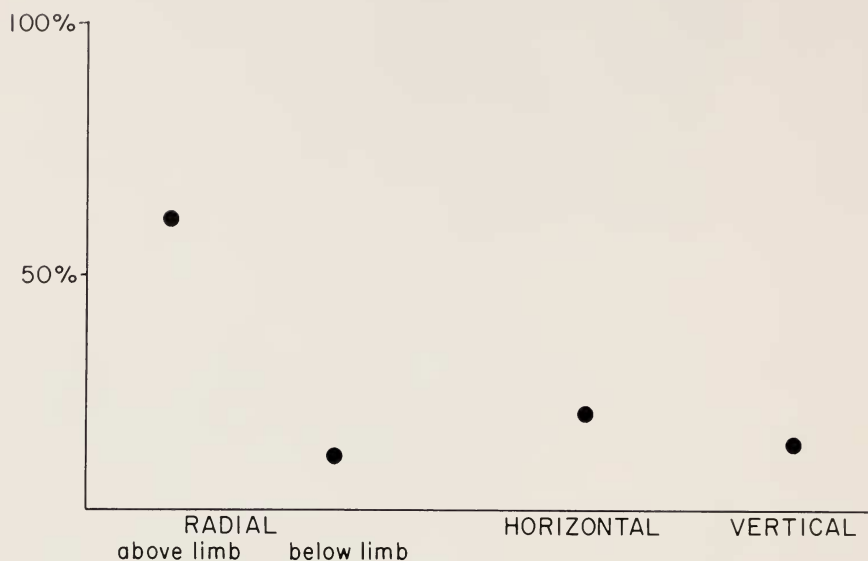


FIG. 4. Movement stereotypy of Panamanian Bananaquits.

between artificial bamboo and squares of cardboard, arranged so as to afford a similar range of light intensities and "hiding places" yielded scores of 0.06, 0.08, 0.16, 0.71, 0.71, and 0.80. Thus, for half of the individuals, the presence of leaves was clearly important (scores of 0.71, 0.71, and 0.80) though strong preferences for any given configuration were, as indicated earlier, not evident. Comparable data for Bananaquits from the mainland are not available, though we should note our impression that, in Panama, Bananaquits are far less ubiquitous than they are in the West Indies. In Panama they appear to be restricted to the forest edge and home gardens. MacArthur (1965) has also suggested this in pointing to the increased "between-habitat" differences on the mainland as compared with nearby islands.

Motor patterns of tropical mainland and island species.—Figures 3 and 4 indicate variations in motor patterns of the Puerto Rican and Panamanian Bananaquits. Despite the variety of habitats in which the former is found, the similarity in its patterning of movements within all these habitats is striking. The timing of movements, however, is less stereotyped, as is seen in Figures 5 and 6, in which are graphed the duration of feeding bouts in different habitats. (By "feeding bout" is meant the period from one flight to the next, during which period feeding occurs more or less continuously.)

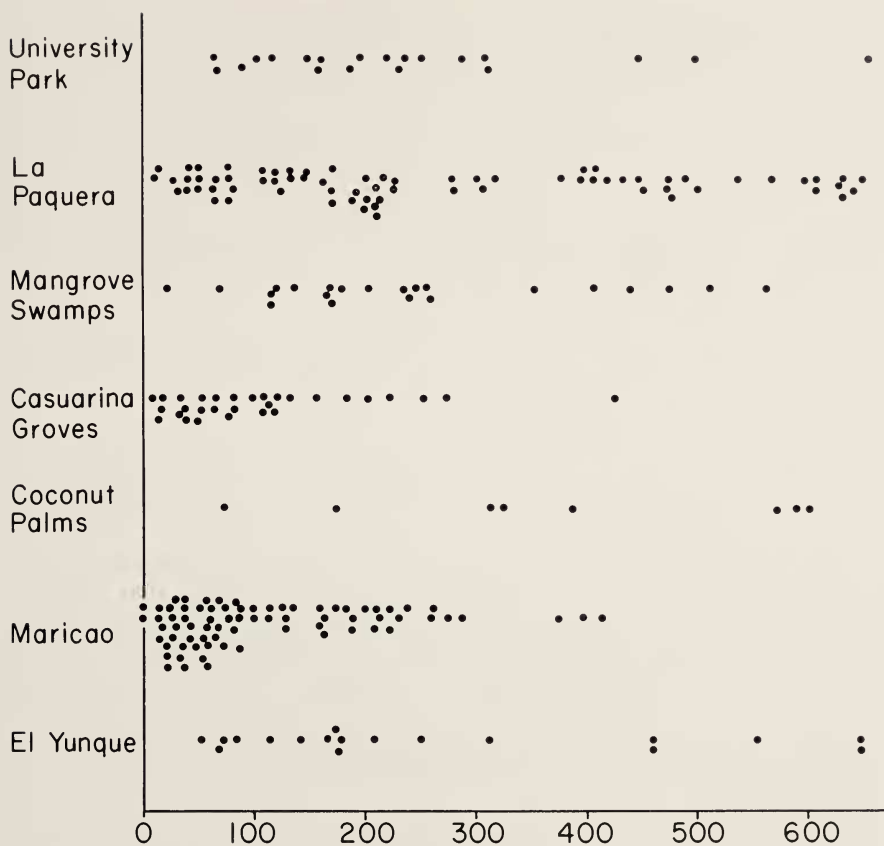


FIG. 5. Duration of feeding bouts of Puerto Rican Bananaquits.

There are some significant inter-habitat variations in this measure (specifically, Maricao vs. La Paquera, Median test, Tate and Clelland, 1957), presumably reflecting differences in the kind and amount of food available. Thus, these birds do make certain adjustments to the nature of their habitat. The data for the mainland Bananaquit show a basically similarity to Bananaquits at Maricao, P. R., both with regard to movements and duration of feeding bouts. The Maricao habitat appears, at least superficially, the most similar of any of those on Puerto Rico to the Bananaquit habitat in Panama.

On the artificial trees, neither wild-trapped Bananaquits (Dominica) or Blue Tanagers (Panama) adhered to the pattern of movements characteristic in nature. Radial movements were virtually nonexistent: Bananaquits' movements were principally in the horizontal plane (63 per cent); those of the tanagers almost evenly divided between horizontal and vertical (54-46 per

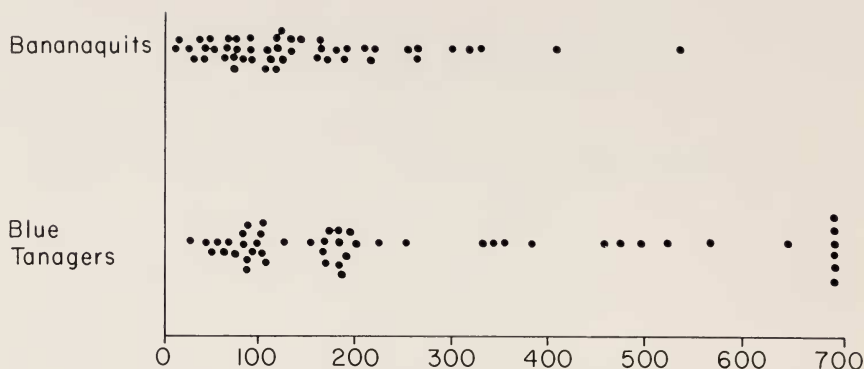


FIG. 6. Duration of feeding bouts of Panamanian birds.

cent). This does not support the notion that these birds are incapable of modifying the pattern of their movements.

Motor patterns of temperate mainland and island species.—Figure 7, taken from Crowell, illustrates in a somewhat different manner, the feeding methods of three species of passerines common both to the eastern U.S. and the island of Bermuda. The differences between island and mainland populations were significant (Chi square, $P < 0.001$). Mainland Cardinals and Catbirds showed a greater diversity of feeding methods than did their island counterparts; the reverse was true for the vireo. It is not yet known whether the increased feeding diversity reflects changes in the behavior of single individuals or different degrees of polymorphism (more strictly, polyethism) in the population as a whole. Since Crowell's mainland observations were not limited to a small area, this is a point that must be examined.

DISCUSSION

It is premature to interpret these results as either favoring or invalidating our hypothesis concerning the causes of tropical diversity. Samples including far more individuals and species will first be needed to fill gaps in the experimental design. However, a number of interesting, if tentative, conclusions can be drawn from these data.

To begin with, given a situation in which the number of potentially competing species is reduced, as occurs on islands with an impoverished fauna, at least one tropical species (specifically, the Bananaquit) apparently has no difficulty expanding into habitats in which, on adjacent mainland, it does not occur. By "habitat" we mean morphologically defined (generally in terms of foliage-height diversity) plant assemblages. On continental land masses such assemblages have particular bird species associated with them

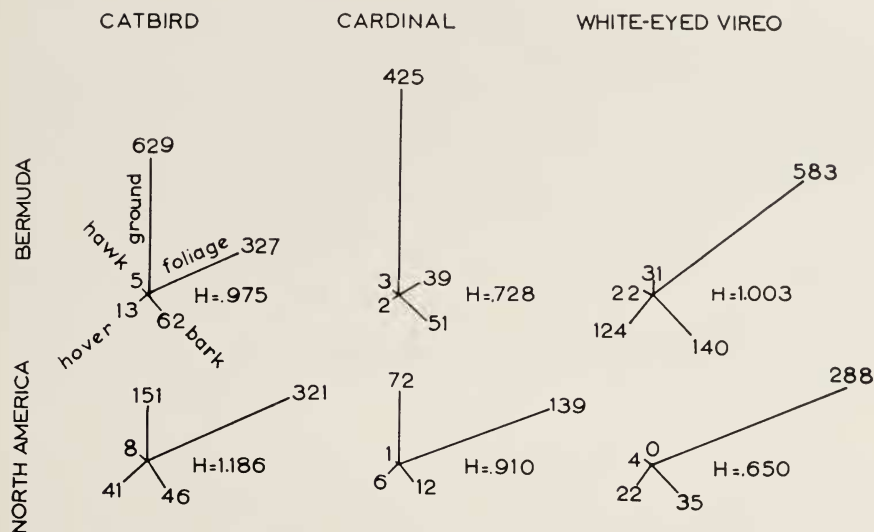


FIG. 7. Crowell's (1962) comparison of the feeding methods (pecking off ground, foliage-gleaning, bark-gleaning, feeding while hovering, hawking) of Catbirds, Cardinals, and White-eyed Vireos in North America and on Bermuda. The numbers show the frequency of the feeding method as observed at 10-second intervals; H is the measure of diversity in feeding methods.

(MacArthur, pers. comm. and 1965). Either these island birds show less selectivity in their choice of habitat or else the features of different habitats relevant to them are not associated with foliage-height diversity, as on the mainland. The data here presented (and those of Crowell, 1962 and MacArthur, 1965) suggest the former to be more likely. Thus, while as a consequence of early learning experiences, tropical birds may in fact prove more "stereotyped" in their actual behavior than temperate zone species (Klopfer, 1965), the responses of these same tropical birds on islands indicates they have a tremendous capacity for "plasticity." That this is a true ontogenetic plasticity is evident from the catholicity shown by the hand-reared birds. Thus, it would appear that while tropical species on tropical mainlands are in fact "stereotyped," this is more likely an effect rather than a cause of their greater diversity.

SUMMARY

The foliage preferences of hand-reared tropical birds are relatively broad. Exposure to a particular type of foliage narrows these preferences. Previous experiments (Klopfer, 1965) had shown that certain temperate zone birds had narrower preferences whether wild-trapped or hand-reared.

The motor patterns of tropical species were shown capable of considerable modification.

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